

ZOOLOGISCHE MEDEDELINGEN

UITGEGEVEN DOOR HET

RIJKSMUSEUM VAN NATUURLIJKE HISTORIE TE LEIDEN

(MINISTERIE VAN CULTUUR, RECREATIE EN MAATSCHAPPELIJK WERK)

Deel 53 no. 28

29 juni 1979

A CHARACTER ANALYSIS OF THE SPECIES OF *SYNERGUS* HARTIG, SECTION II (MAYR, 1872) (HYMENOPTERA, CYNIPIDAE)

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With 83 text-figures

ABSTRACT

A survey is given of the characters used for the differentiation of the species of *Synergus* Hartig, classified with section II of Mayr. Special attention is given to the phenology of the species, for each of which the life-cycle is schematized, with differentiation in spring- and summer-generation. Two forms, provisionally indicated A and B, could not satisfactorily be identified with any of the known species. Sp. B is a common inquiline of oak-apples; biological observations were made on the larvae. *Synergus mutabilis* Dettmer, 1924, is synonymized with *Synergus albipes* Hartig, 1841.

The identification of the species of *Synergus* Hartig, 1840, is notoriously difficult, particularly of those classified in section II (Mayr, 1872). The species of section I, single brooded, that winter in galls as late-stage larvae or pupae and emerge in early summer, are easier to be identified (Eady, 1952). Some of the difficulties with section II may stem from the fact that many species produce two broods in one year, often dissimilar in appearance (Ross, 1951). It should be stated that in all instances the correlations of spring and summer generations were deduced from circumstantial evidence: no specimens were actually reared from one generation to another. Even more confusing than the alternation of broods may be the great variation presumably caused by differences in quantity or quality of larval food. The result of all this is that no character alone is indicative of specific identity and the need for a character analysis is apparent.

The present paper is based on specimens reared from galls collected in the years 1967-1978 in The Netherlands; this material is being preserved in the Rijksmuseum van Natuurlijke Historie, Leiden. Some data were taken from the Dettmer-collection, property of the Natuurhistorisch Museum at Maas-

tricht. Dettmer (1924), not being acquainted with the extended range of variation caused by the occurrence of double broods, described several new species. One of these, i.e., *Synergus mutabilis* Dettmer, is synonymized with *Synergus albipes* Hartig, 1841. Some of my specimens were compared with the material treated by Eady & Quinlan (1963), preserved in the British Museum (Natural History), London. The kind help of C. van Achterberg (Leiden Museum), F. N. Dingemans-Bakels (Maastricht), J. S. Noyes and J. Quinlan (London), in making available for my study the material here treated, is thankfully acknowledged.

CHARACTER ANALYSIS

Since Tavares (1920) and Ross (1951) there is considerable knowledge of the variation in *Synergus*, but this information is not easily used because of the lack of comparative illustrations. Some of these were given by Eady & Quinlan (1963), but only for characters used in their key, which makes it difficult to properly weigh all possible identifications one against the other. The present paper bears the weight of plentiful illustration also for non-differential characters, since this may allow of a balanced evaluation of all possible identifications.

In tabulating the character-states, I record the mean of at least ten typical specimens (five males and five females); in some of the tables the variation is being classified in the rows. The names of the species are abbreviated according to the following list, which at the same time shows their grouping into four alliances. Attention is drawn to the division of some species in spring- (p) and summer-broods (s).

pall. — *Synergus pallicornis* Hartig, 1841

inc. — *S. incrassatus* Hartig, 1840

apic. — *S. apicalis* Hartig, 1841

rot. — *S. rotundiventris* Mayr, 1873

gall. — *S. gallaepomiformis* (Boyer de Fonscolombe, 1832), p & s

sp. A — *Synergus* sp. A

thau. — *S. thaumacerus* (Dalman, 1823)

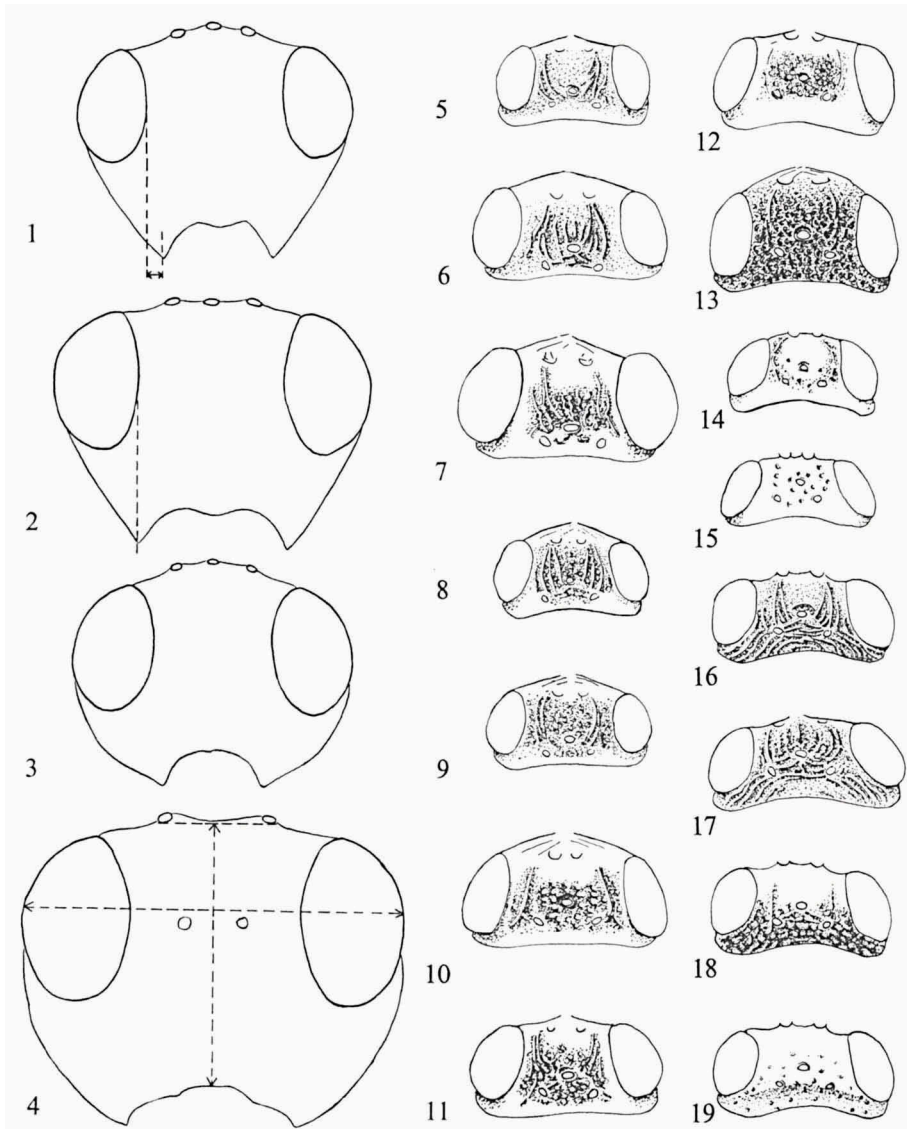
nerv. — *S. nervosus* Hartig, 1840, p & s

alb. — *S. albipes* Hartig, 1841, p & s

sp. B — *Synergus* sp. B

The head

There appears to exist a great variation in several characters of the head, viz., the general shape, the colour, the structure of the frons and vertex, and



Figs. 1-19. Shape of the head (1-4) and structure of frons (5-15) and vertex (16-19) in various species of *Synergus*. 1, *S. pallicornis* ♀ from *Cynips quercusfolii*; 2, *S. albipes* ♂ from *Neuroterus quercusbaccarum*; 3, *S. gallaepomiformis* ♀ from *Andricus kollari*; 4, *S. gallaepomiformis* ♂ from *Andricus fecundator*; 5, *S. albipes* ♂ from *Neuroterus quercusbaccarum*; 6, *Synergus* sp. B ♀ from *Cynips quercusfolii*; 7, *S. gallaepomiformis* ♀ from *Andricus quadrilineatus*; 8, *S. nervosus* ♀ from *Andricus quadrilineatus*; 9, *S. nervosus* ♂ from *Andricus quadrilineatus*; 10, *S. gallaepomiformis* ♀ from *Andricus fecundator*; 11, *S. gallaepomiformis* ♀ from *Andricus quadrilineatus*; 12, *S. gallaepomiformis* ♀ from *Andricus quercusramuli* f. *autumnalis*; 13, *S. incrassatus* ♂ from *Andricus sieboldi*; 14, *S. apicalis* ♀ from *Andricus sieboldi* f. *poissoni*; 15, *S. rotundiventris* ♀ (caught in flight); 16, *S. pallicornis* ♀ from *Cynips quercusfolii*; 17, *Synergus* sp. B ♀ from *Cynips quercusfolii*; 18, *S. gallaepomiformis* ♀ from *Trigonaspis megaptera*; 19, *S. apicalis* ♀ from *Andricus quercusradicis* f. *trilineatus*. Magnification: figs. 1-4, $\times 47$; 5-13, 15-18, $\times 25$; 14, 19, $\times 37$.

the shape of some of the antennal segments: these characters will be discussed in this sequence.

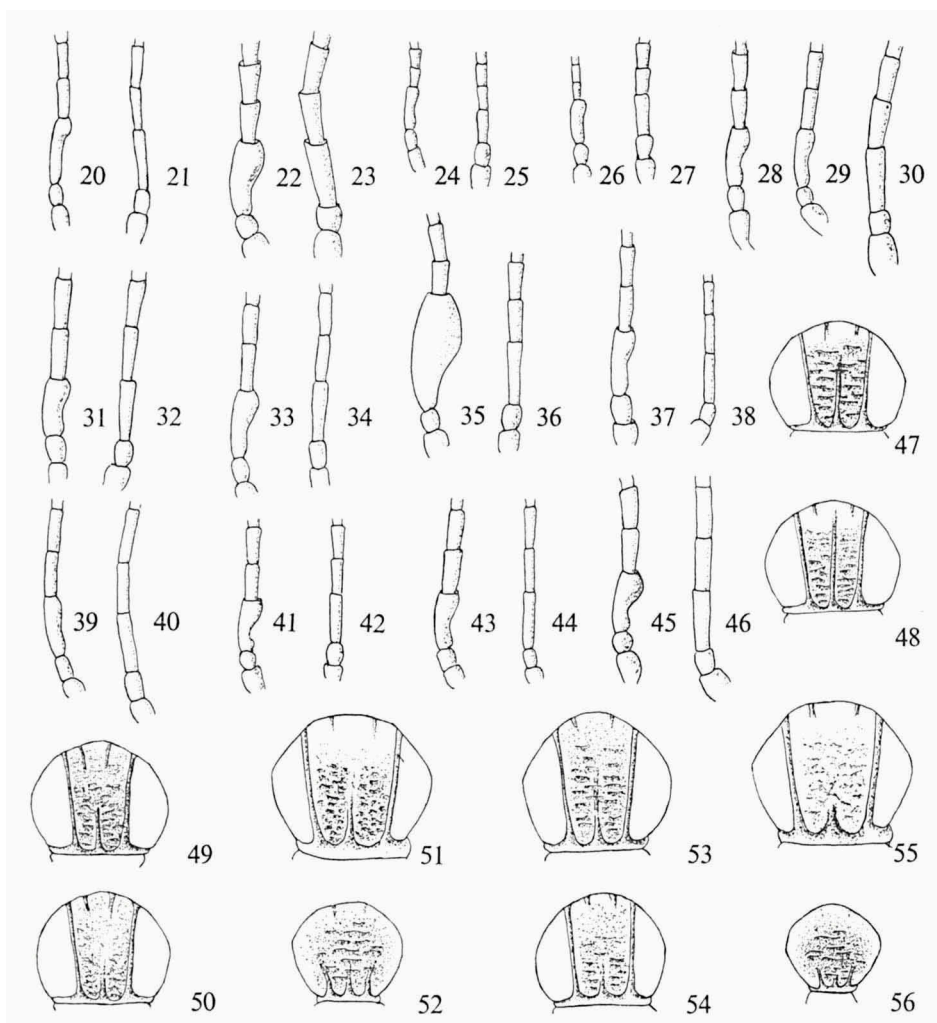
General shape. — In all instances the width of the head (measured across the compound eyes) is larger than the length (measured from an imaginary line connecting the lateral ocelli to the epistomal edge, see fig. 4), but the ratio may vary from 1.3 to 1.6 (table 1). In general, the shape of the head is mainly determined by the form of the cheeks, which may be straight and then more (fig. 1) or less convergent (fig. 2), or buccate, viz., ovate (fig. 3) or rounded (fig. 4). Exact measurements of these differences proved to be difficult, but generally any specimen could be alluded to one of the four alternatives mentioned (table 2).

Colour. — Usually, the head is brown to black, but yellow- and red-coloured forms occur (a similar polymorphism is found in the veins of the wings); males and smaller female specimens may be lighter than normal, and larger specimens sometimes appear rather dull. The antennae are uniform orange, light brown or dark brown, but these are also wasps in which the dark brown segments have a lighter basis and apex (table 3).

It should be stated that colour differences may depend on temperature (possibly in relation to humidity) of the surroundings, as is illustrated by breeding experiments with *S. gallaepomiformis* (p. 312) and *thaumacerus* (p. 315).

Structure of frons and vertex. — Useful characters are the presence or absence of carinae and pits, the area in between being either alutaceous or coriaceous. The carinae may run from the base of the antennae to the lateral ocelli (fig. 5); a number of carinae may also occupy the whole frons or, in some cases interrupted, occur between the lateral and anterior ocelli (fig. 6). Where pits are placed closely together on the frons, they may form an irregular line (fig. 7); sometimes carinae and shallow pits are mixed (fig. 8). The variation may be rather large in a series of wasps bred from one gall, probably descendants of one ovipositing female (figs. 8-9, *S. nervosus*). *S. gallaepomiformis* emerging from various galls in spring, has many pits close together, with either weak or strong lateral carinae (figs. 10-11). Occasionally, the lateral carinae are replaced by rows of pits, with low parts of carinae in between (figs. 13-15, various species). A survey of the characters of the frons is given in table 4.

On the vertex the same characters are present. Carinae occur, for instance, on the vertex of *S. pallicornis* (fig. 16) and spec. B (fig. 17); this shows that quite different species of wasp may be indistinguishable on the structure of the vertex. The character-states are tabulated in table 5, some are figured in figs. 18-19.



Figs. 20-56. Second to fifth antennal segments (20-46) and structure of mesoscutum (47-56) in various species of *Synergus*. 20, 21, *S. pallicornis* from *Cynips quercusfolii*: 20, ♂, 21, ♀; 22, 23, *S. incrassatus* from *Andricus quercusradicis*: 22, ♂, 23, ♀; 24, 25, *S. apicalis* from *Andricus quercusradicis* f. *trilineatus*: 24, ♂, 25, ♀; 26, 27, *S. rotundiventris* from *Callirhytis bella*: 26, ♂, 27, ♀; 28, *S. gallaepomiformis* ♂ from stunted acorns; 29, 30, *S. gallaepomiformis* from *Andricus fecundator*: 29, ♂, 30, ♀; 31, 32, *S. gallaepomiformis* from *Biorhiza pallida*: 31, ♂, 32, ♀; 33, 34, *Synergus* sp. A from *Andricus kollari*: 33, ♂, 34, ♀; 35, 36, *S. thaumacerus* from *Trigonaspis megaptera*: 35, ♂, 36, ♀; 37, 38, *S. nervosus*: 37, ♂ from *Neuroterus quercusbaccarum* f. *lenticularis*, 38, ♀ from *Cynips longiventris*; 39, 40, *S. nervosus* from *Andricus nudus* f. *malphigii*: 39, ♂, 40, ♀; 41, 42, *S. albipes*: 41, ♂ from *Trigonaspis megaptera* f. *renum*, 42, ♀ from *Andricus corruptrix*; 43, 44, *S. albipes* from *Andricus curvator*: 43, ♂, 44, ♀; 45, 46, *Synergus* sp. B from *Cynips quercusfolii*: 45, ♂, 46, ♀. 47, *S. incrassatus* ♀ from *Andricus sieboldi*; 48, *S. thaumacerus* ♀ from *Trigonaspis megaptera*; 49, 50, *S. nervosus* from *Andricus quadrilineatus*: 49, ♀, 50, ♂; 51, *Synergus* sp. B, ♀ from *Cynips quercusfolii*; 52, *S. rotundiventris* ♀ (caught in flight); 53, 54, *S. pallicornis* from *Cynips quercusfolii*: 53, ♀, 54, ♂; 55, *Synergus* sp. B, ♂ from *Cynips quercusfolii*; 56, *S. rotundiventris* ♀ from *Callirhytis bella*. Magnification: 20-46, \times 47; 47-55, \times 25; 56, \times 37.

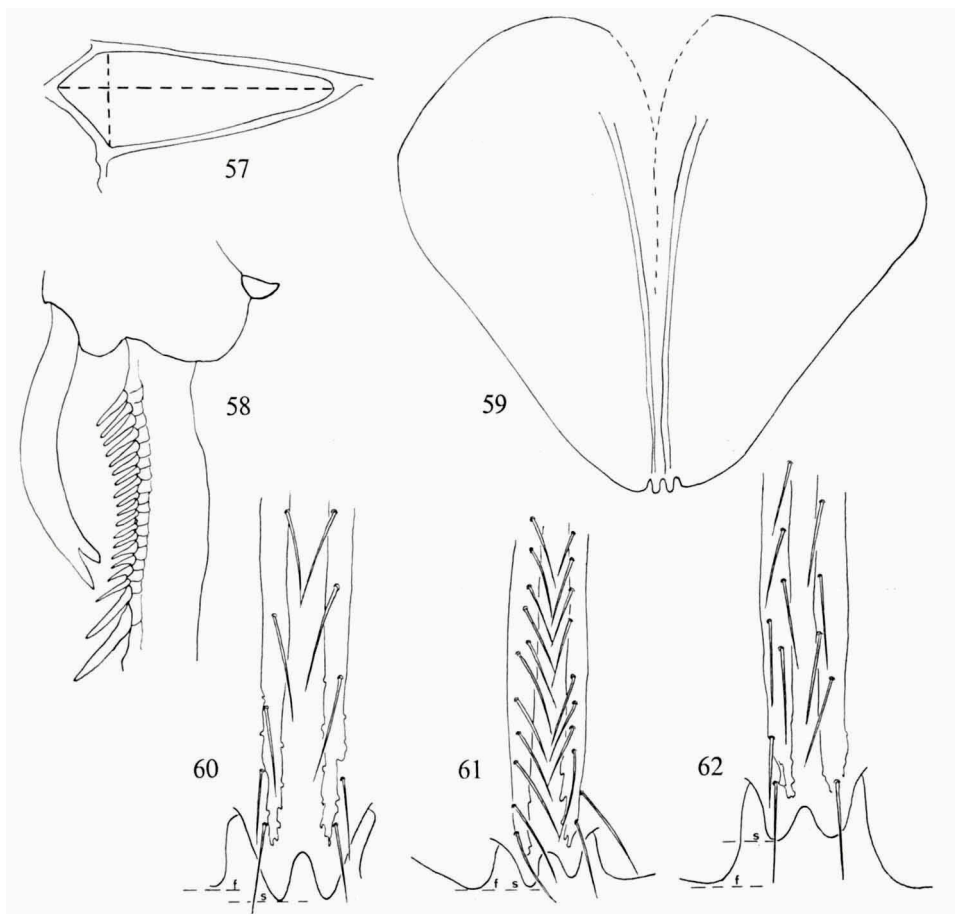
Antennal segments. — The shape of the complete antennae was sometimes used as a differential character. In my opinion, this is not right in all cases as especially in larger specimens the antennae may be filiform, whereas they are clavate in smaller examples of the same species. The proportions of the third, fourth and fifth segments in relation to those of the second, are of some use (table 6), e.g., the third segment is rather long in males of a number of species (*S. pallicornis*, *incrassatus*, *thaumacerus*, sp. B), while in another the fourth is very short (*S. apicalis*); in the females, the third segment is large in relation to the fourth in the same species mentioned above, but the two segments are subequal in others (*S. gallaepomiformis*, *nervosus* p, *albipes* s).

The excavation of the third antennal segment in the male is characteristic of some species (figs. 20-45, males), although it is quite similar in others. In three species, the male as well as the female second antennal segment is almost globose (*S. rotundiventris*, *albipes*, sp. B) or even transverse (*incrassatus*), but usually it is more distinctly oblong (e.g., *S. pallicornis*, *thaumacerus*, *nervosus*).

The thorax

Mesoscutum. — The transverse carinae of the mesoscutum vary from sharp distinct wrinkles with wide and shiny interspaces, as seen in *S. incrassatus* (fig. 47), to coriaceous transverse rugae (*S. thaumacerus*, see fig. 48, and *gallaepomiformis*), or there are faint rugae on a coriaceous surface (figs. 49-51); see table 8. The variation in the length of the median scutal line is given in table 7. In contrast with the mesoscutal surface the median scutal line bears no setae; as these are also absent from a stretch of what therefore appears to be an extension of the medial scutal line, this length may be difficult to measure. The line is nearly complete, or its length is almost three-quarters of the length of the mesoscutum, in *S. gallaepomiformis* and *thaumacerus* (fig. 48). Somewhat smaller and shorter (up to half the length of the mesoscutum) are the lines in *S. nervosus* (figs. 49, 50). The median scutal line of *S. pallicornis* (fig. 53) is interrupted and reaches to half the length of the mesoscutum in most females; in males it is often shorter (fig. 54). In many instances a larger length is correlated with a greater width, but a median scutal line shaped like a short wide triangle (fig. 55) does also occur.

In two species the notaulices are obsolete for more than half of their length (figs. 52, 56). When reared from some hosts the notaulices of *S. rotundiventris* are much variable: specimens reared from galls of *Callirhytis bella* have half-length notaulices instead of the usual length of one-quarter of the mesoscutum.



Figs. 57-62. Wing (57), apex of fore tibia (58), and hypopygium (59-62) of various species of *Synergus*. 57, *S. albipes* ♀ from *Neuroterus quercusbaccarum*; 58-60, *S. incrassatus*, ♀ from *Andricus sieboldi*; 61, *S. pallicornis* ♀ from *Cynips quercusfolii*; 62, *S. albipes* ♀ from *Neuroterus quercusbaccarum*. Magnification: 57, 59, $\times 47$; 58, 60-62, $\times 240$.

Wings. — Eady & Quinlan as well as Tavares sometimes used the length and width of the radial cell without exactly indicating how it was measured. My measurements (fig. 57) are given in table 9. Short radial cells are seen in the summer-generation of *S. nervosus* and the males of *S. incrassatus*; long ones in *S. apicalis*, *rotundiventris* and the females of *S. pallicornis* and *thaumacerus*.

Legs. — I counted the number of spines on the tibia of the fore leg, but it does not seem to be of any use. Although *S. pallicornis* has relatively few spines and *gallae-pomiformis* more, there is a certain overlap (fig. 58, table 10).

The gaster

Female gaster. — The shape of the apparent first gastral segment (actually the combined second and third abdominal segments) is almost rounded posteriorly when seen in lateral aspect, except for one species where it is more angular (*S. apicalis*).

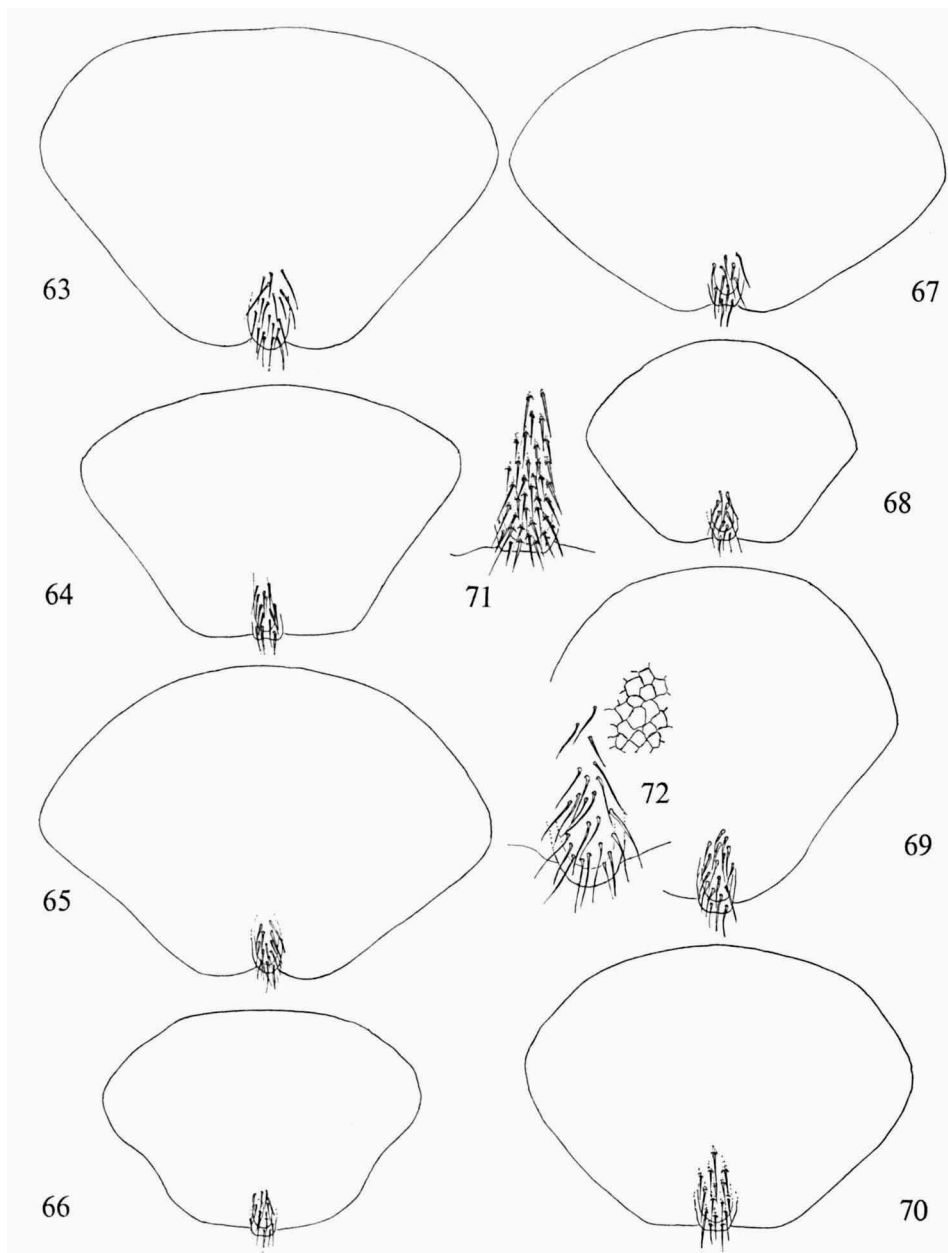
Little dots (Ross, 1951: 86) form a patch at the apex, or a row along the posterior edge; in many instances they are completely absent. Two characters were obtained from the hypopygium (fig. 59), viz., the length of the spine (s) relative to the length of the lateral flanges (f): the spine protrudes as in *S. incrassatus*, *apicalis* and *rotundiventris* (fig. 60); the spine and the flanges extend to the same length (*S. pallicornis*, *gallaepomiformis*, *thumacerus* and sp. A; fig. 61); or the flanges protrude beyond the apex of the spine (*S. albipes*, *nervosus* and sp. B; fig. 62).

The length of the V-shaped ridges and the number of setae along the "arms" of the V have a great overlap for the various species, but it is clear that *S. incrassatus* and sp. A have a large number of setae on a relatively short V, as in contrast with *S. incrassatus*, which has a small number on a long V. The other species are intermediate (table 11).

Ventral plate of the male. — Kierych (1963) used the shape of the ventral plate of the male for discrimination of some species, but the thin borders of the plates make it very difficult to determine the real shape. It is, however, possible to distinguish two types, viz., 1, the greatest width lays above the middle of the plate (*S. pallicornis*, *thumacerus* and sp. A; figs. 63, 64, 66); and 2, the greatest width is across the middle of the plate (the other species; figs. 65, 67-70).

The last sternite (the ventral plate) bears a distal oval area, set with shorter or longer setae; some species have these setae implanted on small protuberances that are distinctly pigmented (fig. 71) (*S. incrassatus*, *apicalis*, *rotundiventris*). Even in the two last-mentioned species, which consist of tiny specimens, this character is very distinct, while in the other species the oval patch is less pigmented and it does not bear protuberances (e.g. sp. B, fig. 72). Also visible in some species (*S. gallaepomiformis*, *albipes*, sp. B; see fig. 72) is the hexagonal structure of the surface of the ventral plate, which is not seen in the other species.

The male genital apparatus was described by Schulz (1961). She noticed a variation in several characters, which she considered differential for some of the species, only two of which belong to our section II. The variation in my material proved to extend beyond the boundaries of the two species concerned, i.e., *S. gallaepomiformis* and *pallicornis*. In some specimens I even found a difference between two sides, e.g., in the number of claws on the claspers (table 12).



Figs. 63-72. Ventral plate of the male of various species of *Synergus*. 63, *S. pallicornis* from *Cynips quercusfolii*; 64, *S. thaumacerus* from *Trigonaspis megaptera*; 65, *S. gallaepomiformis* from *Andricus kollari*; 66, *Synergus* sp. A from *Andricus kollari*; 67, *S. albipes* from *Neuroterus quercusbaccarum*; 68, *S. nervosus* from *Andricus quercusramuli*; 69, *Synergus* sp. B from *Cynips quercusfolii*; 70, *S. incrassatus* from *Andricus quercuscorticis*; 71, *S. apicalis* from *Andricus quercusradicis* f. *trilineatus*; 72, *Synergus* sp. B from *Cynips quercusfolii*. Magnification: 63-70, $\times 96$; 71, 72, $\times 192$.

Tables with measurements and other characters of various species of
Synergus.

<i>Synergus</i>	<i>pall.</i>	<i>inc.</i>	<i>apic.</i>	<i>rot.</i>	<i>gall.p.</i>	<i>gall.s.</i>	<i>sp. A</i>	<i>thau.</i>	<i>neru.p.</i>	<i>neru.s.</i>	<i>alb.p.</i>	<i>alb.s.</i>	<i>sp. B</i>
TABLE I. Ratio length/width of the head.													
male	1.5	1.6	1.4	1.5	1.4	1.4	1.5	1.4	1.4	1.3	1.4	1.5	1.4
female	1.6	1.6	1.4	1.5	1.5	1.4	1.5	1.4	1.4	1.4	1.5	1.5	1.5

TABLE II. Shape of the head (males and females): + usually, + incidentally.													
ovate	.	.	+	+	+	.	+	+
rounded	.	+	+	+	+	+
triangulate/ovate	.	+	.	.	+	+	.	+	+	+	+	+	.
trapezoid	+	+	.	+

TABLE III. Colour of the antennae (males and females): + usually, + incidentally.													
orange	+	.	.	.	+	.	.	+
yellow-brown	.	+	+	.	+	+	+	+	.
dark brown	.	.	+	+	.	+	+
black	+
apices light	+	.	.	+	.	.	.	+

TABLE IV. Characters of the frons (males and females): + usually, + incidentally.													
carinae absent	.	.	+	+
carinae few, weak	.	+	.	.	.	+	+	+	+	.	+	+	+
" distinct, branched	+	.	.	.	+	+	.	+	+	+	.	.	+
punctures absent	+	+	+	+	+	+	+	+
punctures few	.	.	+	+	.	+	+	+	+	+	.	.	.
punctures many	.	+	.	.	+	+
punctures fused	.	+	.	.	.	+

TABLE V. Characters of the vertex (males and females): + usually, + incidentally.													
carinae weak	.	.	+	+	.	.	+	.	+	+	+	+	+
carinae distinct	+	+	.	.	+	+	.	+	.	.	+	+	+
" between ocelli	+	+	+	.	+	+	+
punctures weak	.	.	+	+	.	.	.	+
punctures distinct	.	+	.	.	+	+	.	+
" between ocelli	.	+	.	.	+	+	.	.	.	+	.	.	.

TABLE VI. Ratio length/width of the second antennal segment.													
males	1.6	1.3	1.4	1.0	1.2	1.2	1.2	1.0	1.3	1.3	1.0	1.3	1.0
females	1.4	0.9	1.2	1.5	1.1	1.4	1.4	1.6	1.6	1.6	1.1	1.3	1.3
length of segment, relative to segment 2:													
males	segment 3	4.0	4.0	1.5	1.9	2.5	2.6	3.5	5.0	3.0	2.5	3.2	4.0
	segment 4	2.0	2.0	0.5	1.3	2.0	1.6	2.5	1.5	2.0	2.0	2.2	2.0
females	segment 3	2.5	2.6	1.3	2.0	2.2	2.2	2.6	2.5	2.0	2.7	2.5	2.6
	segment 4	1.7	1.7	1.0	1.3	2.0	2.0	1.8	1.5	1.7	2.0	2.0	2.1

PHENOLOGICAL AND TAXONOMICAL NOTES

In this chapter mainly phenological data are given for *Synergus*-wasps and their larvae, in connection with the life-cycle of their hosts.

The cycles are figured on the basis of a time-bar, while the emergence dates are recorded in tables 13-22. Some comparison is made with records from England (mainly taken from Eady & Quinlan, 1963) and Germany (mainly taken from Weidner, 1960). Incidental earlier and later emergence dates are given in brackets.

In the figures (figs. 73, 74-83) a continuous bar represents the life of the host Cynipid, viz., its agamous generation stippled, its sexual generation shaded. When the galls are visible, the bar is widened; an empty bar indicates the time in which the gall maker has emerged, but the inquiline *Synergus* may still be present in the gall. The life time of *Synergus* is indicated by a black bar. The earliest and latest dates of emergence observed, and the date at which emergence is at its peak, are shown by arrows. Although there were no experiments made relating to the life-span of a mature wasp, it certainly can amount to over three weeks, as was observed for *S. reinhardi* Mayr (section I) and *S. gallae-pomiformis*.

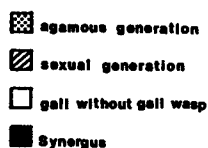


Fig. 73. Symbols used in figs. 74-83.

Synergus pallicornis Hartig (table 13, fig. 74)

The larvae of *S. pallicornis* make secondary chambers in the tissue of the host gall. Thin-walled galls are not suitable for their attack. Most *pallicornis*-wasps were reared from *Cynips quercusfolii* ♀. These galls appear at the end of June (24th; gall diameter 1-2 mm); ovipositing females of *pallicornis* were seen at the same time and in the beginning of July. Eggs are difficult to find in the gall tissue, but first-stage larvae were measured at the end of August (24th; length larva 0.5 mm, gall diameter 7 mm). Full-grown larvae were found at the end of September and in the beginning of October (maximum length 2.7 mm, independent of the gall diameter ¹).

¹) For the relation of the gall diameter and its inhabitants, among which *Synergus pallicornis*, see Wiebes-Rijks (1974).

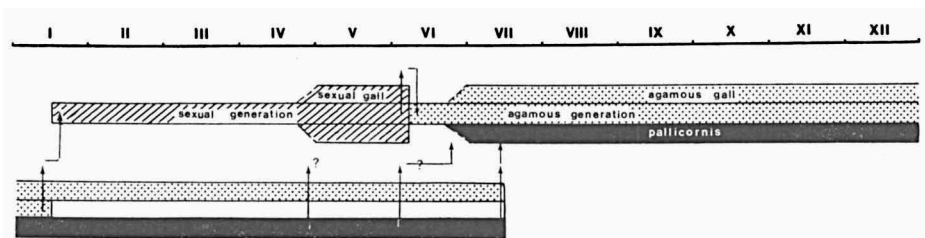


Fig. 74. Life-cycle for *Synergus pallicornis* (black) in the galls of the agamous generation of *Cynips quercusfolii* (stippled).

Tables with host species and phenological data for various species of *Synergus*.

		England	Germany	The Netherlands
TABLE XIII. <i>Synergus pallicornis</i> .				
<i>Cynips quercusfolii</i>	♂	+	+	(24-IV) V-VI (1-VII)
<i>Cynips longiventris</i>	♂	+	+	(10-V) V-VI (16-VI)
<i>Cynips divisa</i>	♂	+	+	(20-IV) V-VI (6-VII)
<i>Cynips disticha</i>	♂	+	+	5-VII
<i>Cynips agana</i>	♂	+	-	-
<i>Neuroterus quercusbaccarum</i> f. <i>lenticularis</i>	♂	-	-	15-VII
<i>Andricus curvator</i> f. <i>collaris</i>	♂	-	-	20-IV
<i>Andricus albopunctatus</i>	♂	-	-	26-VI
<i>Andricus corruptrix</i>	♂	-	-	15-V, 20-V
<i>Andricus quercuscalicis</i>	♂	-	-	15-VII
TABLE XIV. <i>Synergus incrassatus</i> .				
<i>Andricus quercusradicis</i>	♂	+	+	(1-IV) V-VI (19-VII)
<i>Andricus sieboldi</i>	♂	+	+	(8-V) V (29-V)
<i>Andricus quercuscorticis</i>	♂	+	-	(21-IV) V (15-VII)
TABLE XV. <i>Synergus apicalis</i> .				
<i>Andricus quercusradicis</i> f. <i>trilineatus</i>	♂♀	+	-	(18-V) VI (18-VII)
TABLE XVI. <i>Synergus rotundiventris</i> .				
<i>Andricus quercusradicis</i> f. <i>trilineatus</i>	♂♀	+	-	-
<i>Andricus kollari</i>	♂	-	-	28-V
<i>Andricus corruptrix</i>	♂	-	-	10-V, 4-VI
<i>Callirhytis bella</i>		-	-	(18-V) V (20-VI)

In galls of *Cynips quercusfolii*, *pallicornis* may remain in larval diapause until young galls of the next agamous generation are available, and thus overcome the period of the sexual *taschenbergi*-generation of *Cynips*. There are, however, also some early emergences at the end of April, which would need an alternative host. At that time, the only alternatives with relatively thick walls are *Andricus curvator* ♂♀ and *Neuroterus quercusbaccarum* ♂♀, but no *pallicornis* were reared from galls of these species. The flight period for *pallicornis* in England was recorded by Askew (1961, fig. 6) to last from the end of May to the beginning of October.

Synergus incrassatus Hartig (table 14, fig. 75)

The larvae of *S. incrassatus* develop in the chambers of the plurilocular gall of *Andricus quercusradicis* 8. They live with two or three in one chamber, which they subdivide by thin walls; the host larva is being squeezed to death. Galls of *quercusradicis* are light-coloured and very soft in the first year of their existence. By dissecting these galls I found no *Synergus*-eggs nor larvae. The second-year galls are brown-coloured and they are much harder; in these galls I found young *Synergus*-larvae, while in the third year I found wasps

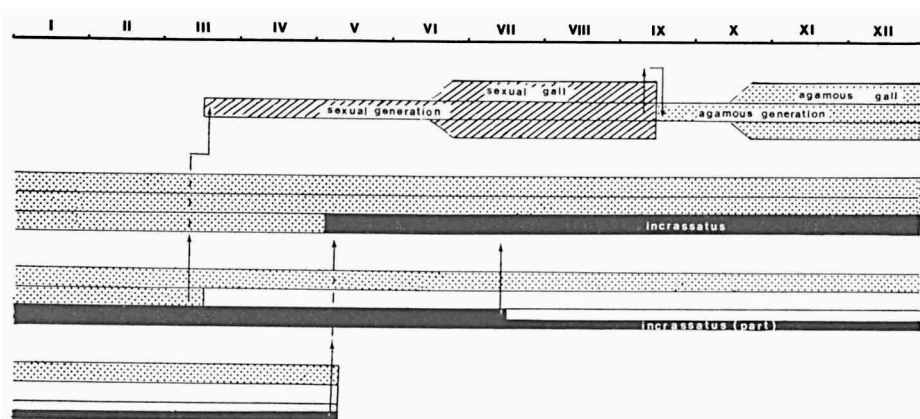


Fig. 75. Life-cycle for *Synergus incrassatus* (black) in the galls of the agamous generation of *Andricus quercusradicis* (stippled).

as well as full-grown larvae. Thus, specimens of *incrassatus* may emerge in the third year of the host gall as well as in the fourth: a gall collected in the summer of 1976 yielded wasps on the 15th of July, 1977, and again, in a smaller number, on the 18th of May, 1978. The long growing period of *quercusradicis* galls makes it possible that the second-year summer-emergences (third year of the host gall) as well as the third-year spring-emergences

(fourth year of the host gall) can find a suitable host again in *A. quercusradicis*. From the hosts *A. quercuscorticis* ♂ and *sieboldi* ♂ I reared wasps in the third year of the gall only.

Synergus apicalis Hartig (table 15, fig. 76)

I reared the wasps of *S. apicalis* from *Andricus quercusradicis* f. *trilineatus* ♂♀ galls only. There are some specimens in Dettmer's collection labelled to have been reared from galls of *A. inflator* ♂♀ and *A. fecundator* ♂, but these may have been composite structures, caused by succession of eggs of different species laid in one and the same bud also infected by *A. quercusradicis* ♂ (Wiebes-Rijks, 1976: 70-71). There is one larva per host gall. Overwintering as a larva usually lasts until the end of March (30th), although there are full-grown wasps in some galls as early as March 7th. Emergences of *apicalis*-wasps are mainly seen in June, when the new generation of the same host is already available: thus, *S. apicalis* needs no alternative host.

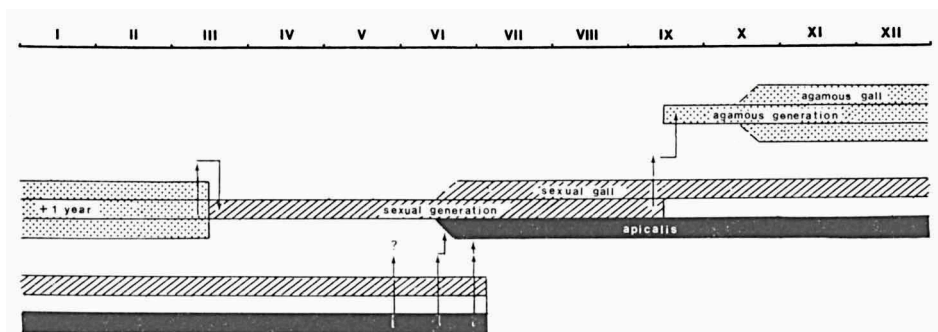


Fig. 76. Life-cycle for *Synergus apicalis* (black) in the galls of the sexual generation of *Andricus quercusradicis* (f. *trilineatus*) (shaded).

Synergus rotundiventris Mayr (table 16, fig. 77)

This species I mainly reared from buds of *Quercus robur* containing galls of *Callirhytis bella*. By dissecting *robur*-buds in February I found full-grown larvae of *bella* as well as larvae of *rotundiventris*, in different buds. Adults of *rotundiventris* were reared in May and June. At that time, the only available host is *Andricus quercusradicis* f. *trilineatus* ♂♀, from which the species was recorded (Eady & Quinlan, 1963). Possibly the galls of *Andricus kollari* ♂ and *A. corruptrix* ♂, listed in table 16, actually were earlier gall chambers of *A. quercusradicis* f. *trilineatus*. In fig. 77 the generation of *C. bella* is supposed to be a sexual one.

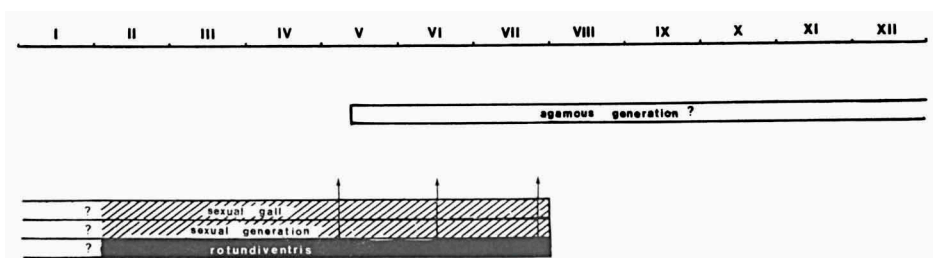


Fig. 77. Life-cycle for *Synergus rotundiventris* (black) in the galls of *Callirhytis bella* (probably, sexual generation).

Synergus gallaepomiformis (Boyer de Fonscolombe) (table 17, fig. 78)

In the autumn of 1976, galls of *Andricus quercusramuli* f. *autumnalis* ♂ were heavily parasitized by *S. gallaepomiformis*. Galls collected at October 9th were dissected and the larvae were kept in glass-tubes during two months, under natural conditions. Then, at December 9th, a sample of eight larvae originating from one and the same gall, were divided into two lots, viz., four were reared indoors (temperature ca. 20° C, rather dry conditions) and four were kept under natural conditions (ca. 8° C, relatively humid). Those kept indoors rather quickly (December 22nd) yielded wasps with yellow faces and light antennae, conform the normal summer-generation; those kept under more natural conditions developed into the blackish spring-generation at the normal emerging date (May, 1977).

This experiment, as well as that to be discussed below with *S. thaumacerus*, consolidates Ross' (1951) supposition that a yellow-faced generation in

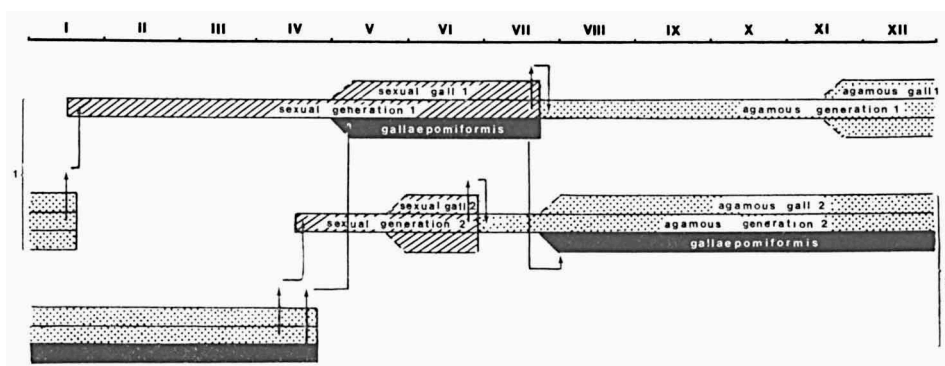


Fig. 78. Life-cycle for *Synergus gallaepomiformis* (black) in the galls of the sexual generation of *Biorhiza pallida* (shaded) and in those of the agamous generation of *Andricus fecundator* (stippled).

summer (s) alternates with a black-faced one in spring (p). The differences between the two generations are more distinct in *S. gallaepomiformis* than in other species of *Synergus*. The following field observations make clear that the differences in colour between the two generations are due to differences in temperature: *gallaepomiformis*-wasps from galls of *Andricus quadri-lineatus* ♂ growing in shaded situations are almost black, although exposed galls yield the yellow-faced summer-generation. A similar observation was made for *A. albopunctatus* ♂.

For late summer galls such as *A. solitarius* ♂ and *A. fecundator* ♂, it is known that a part of the larvae of *Synergus* quickly develop into a yellow-faced first-year generation and that the other part emerges in the following spring as a black-faced second-year generation. By the possibility of spreading the emergences over more than half a year, a large range of alternative host galls can be attacked. In fig. 78 the summer-generation is situated in the sexual generation of *Biorhiza pallida* and the spring-generation in the agamous generation of *Andricus fecundator*.

Synergus sp. A (table 18, fig. 79)

Among the various forms of *Synergus* reared, there are two not fully agreeing with any description of named species. Because the possibility cannot be excluded that they will prove to be extreme variants of known species, I indicate them with "A" and "B" rather than formally name them. Controlled rearing experiments over more than one generation must show their true status.

Species A belongs to the alliance of *Synergus gallaepomiformis* and *thaumacerus* (which is at once distinguished by the third antennal segment of the male being inflated distally (fig. 35), but in some aspects also resembles *S. pallicornis* and *nervosus*. It has, however, an ovate head instead of the trapezoid shape of *pallicornis* (fig. 1). The excavation of the third male antennal segment begins before the middle (fig. 33), not just before the apex (fig. 20). There are weak carinae on the vertex. The median scutal line reaches to half (or less) of the length of the mesoscutum. The colour of the legs and antennae is yellow-brown instead of orange.

Punctures on the frons are present as in *gallaepomiformis* (p), although they are sparse and shallow; *gallaepomiformis*, however, has punctures also on the vertex, which are absent in sp. A. The head of *gallaepomiformis* is convex in lateral view, in sp. A it is flat. Differences can also be found in the length of the median scutal line, which is much shorter ($\frac{1}{2}$ to $\frac{1}{4}$ of the length of the mesoscutum) than in *gallaepomiformis* (where it is $\frac{3}{4}$ or more).

Tables with host species and phenological data for various species of
Synergus, continued.

		England	Germany	The Netherlands	
TABLE XVII. <i>Synergus gallaepomiiformis</i> .					
				yellow-faced (s)	black-faced (p)
<i>Cynips quercusfolii</i>	♂	-	-	-	(28-IV) V-VI (24-VI)
<i>Cynips quercusfolii</i> f. <i>taschenbergi</i>	♂♀	-	-	(8-VI) VI (28-VI)	
<i>Cynips longiventris</i>	♂	-	-	-	21-V, 20-VII
<i>Cynips divisa</i>	♂	-	-	-	8-V, 10-V
<i>Andricus ostreus</i>	♂	+	-	24-VIII	24-IV
<i>Andricus curvator</i> f. <i>collaris</i>	♂	-	-	-	16-III
<i>Andricus curvator</i>	♂♀	+	-	30-VIII	-
<i>Andricus solitarius</i>	♂	+	+	(5-VIII) VIII (13-IX)	21-IV
<i>Andricus glandulae</i>	♂	-	-	-	26-VII
<i>Andricus quercusramuli</i> f. <i>autumnalis</i>	♂	-	-	-	(6-V) V (9-VI)
<i>Andricus quercusramuli</i>	♂♀	+	-	26-VI	-
<i>Andricus albopunctatus</i>	♂	+	+	(11-VI) VI (1-VIII)	12-VI, 26-VI
<i>Andricus fecundator</i>	♂	-	+	(9-IX) IX (23-IX)	(30-IV) V (8-V)
<i>Andricus callidoma</i>	♂	+	-	-	20-V
<i>Andricus malphigii</i>	♂	-	-	-	7-IV, 23-IV
<i>Andricus seminationis</i>	♂	+	-	-	-
<i>Andricus quadrilineatus</i>	♂	+	-	(20-VI) VI (1-VII)	(18-VI) VI (28-VI)
<i>Andricus quercusradialis</i>	♂	-	+	-	-
<i>Neuroterus tricolor</i>	♂	+	-	-	-
<i>Neuroterus quercusbaccarum</i> f. <i>lenticularis</i>	♂	-	-	-	5-VII
<i>Neuroterus quercusbaccarum</i>	♂♀	-	+	-	23-VI
<i>Neuroterus numismalis</i> f. <i>vesicator</i>	♂	-	-	-	19-VI
<i>Neuroterus albipes</i> f. <i>laeviusculus</i>	♂	-	-	-	8-VIII
<i>Trigonaspis megaptera</i> f. <i>renum</i>	♂	-	-	-	29-V
<i>Trigonaspis megaptera</i>	♂♀	+	-	20-VII	-
<i>Biorhiza pallida</i>	♂♀	+	+	(28-VI) VII (25-VII)	-
stunted acorns		-	-	4-IX	(30-IV) V (10-VI)

TABLE XVIII. *Synergus* sp. A.

<i>Andricus kollari</i>	♂	-	-	(5-VI) VI (22-VI)
<i>Andricus lignicola</i>	♂	-	-	22-VI
<i>Andricus corruptrix</i>	♂	-	-	15-VI, 17-VI

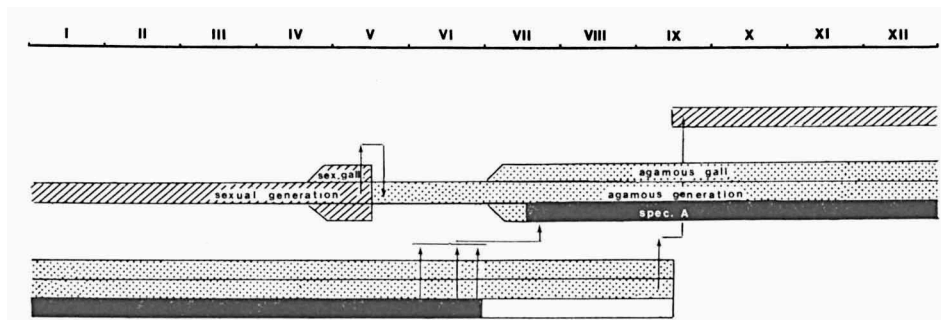


Fig. 79. Life-cycle for *Synergus* sp. A (black) in the galls of the agamous generation of *Andricus kollari* (stippled).

In the presence of shallow punctures on the frons, sp. A resembles *nervosus*, but the third antennal segment of the male has the excavation before the middle, not in the middle as in *nervosus*. The weak carinae of the meso-scutum distinguish sp. A from *nervosus*, where they are irregular.

I reared *Synergus* sp. A mainly from galls of *Andricus kollari* ♂. Young larvae were found in the gall tissue from July 30th onwards, and adults were reared in the second half of June of the next year. From fig. 79 it appears that there is a gap of about a month, which is possibly overcome by the longevity of the wasps.

Synergus thaumacerus (Dalman) (table 19, fig. 80)

A similar breeding experiment as carried out with *S. gallaepomiformis* was made with *S. thaumacerus*. From a *Trigonaspis megaptera* ♂♀ gall with twelve *Synergus*-larvae, found at June 12th, six were kept under natural

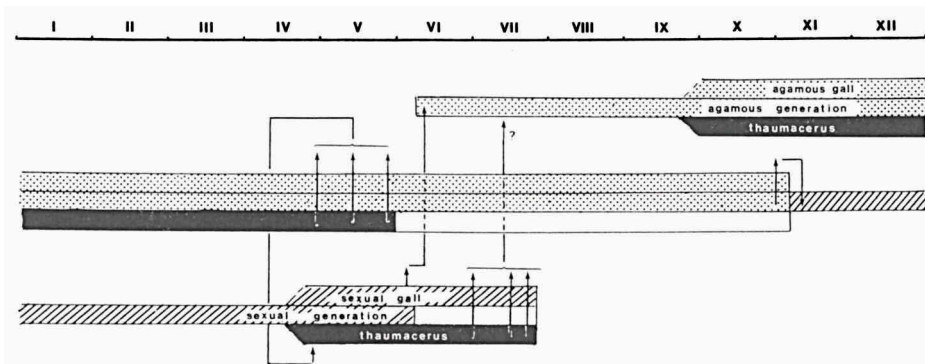


Fig. 80. Life-cycle for *Synergus thaumacerus* (black) in the galls of the sexual generation (shaded) and in the agamous generation (stippled) of *Trigonaspis megaptera*.

conditions and yielded normally yellow- and red-faced *thaumacerus*-wasps at June 30th. The other six were kept at a temperature of ca. 5° C (relatively humid) till July 18th, when four had become uncoloured pupae and two were still larvae. Then they were brought at a more natural temperature: at July 24th, black-faced wasps were found alive in the glass-tube.

It is normal to find the larvae of the summer generation of *S. thaumacerus* with great numbers together in one host gall, i.e., the sexual generation of *Trigonaspis megaptera*; the agamous generation (f. *renum*) is the host for the spring generation of *Synergus*. The cycle seems almost synchronized with that of the host. There is, however, an interval of nearly three months, in which neither host nor parasite can be found: they may be present as eggs in the oak-leaves.

Synergus nervosus Hartig (table 20, fig. 81)

The larvae of the summer generation of *S. nervosus* were found in agamous galls of *Andricus quadrilineatus*, as early as May 30th. At that time the larvae of the host were much smaller (i.e., 3.5 mm long, 2 mm wide) than those of *nervosus* (6.5 × 4 mm). The inquilines grow fast and emerge when the agamous generation is available of galls such as *Cynips longiventris* ♂, where- in the following spring-generation of *Synergus* can develop. Some galls, e.g. of *Andricus ostreus* ♂, may yield a summer-generation of *nervosus* as well as a spring-generation in the next year.

There is some overlap in the emergence dates of the spring- and summer- generations, e.g., June 21st for the spring-generation from galls of *Andricus*

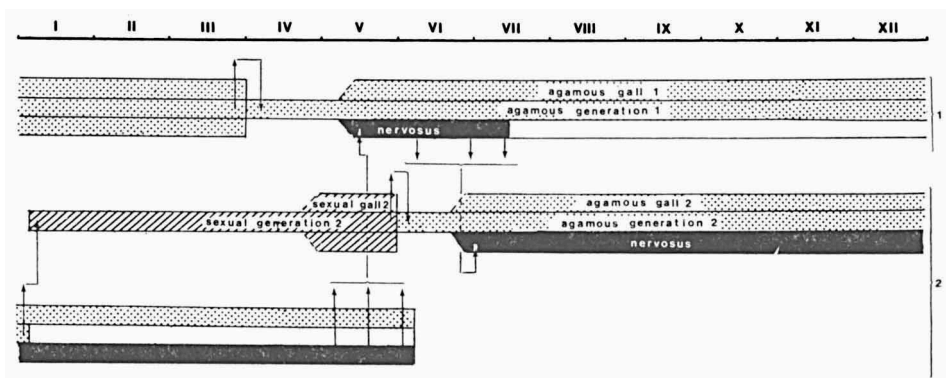


Fig. 81. Life-cycle for *Synergus nervosus* (black) in the galls of the agamous generation of *Andricus quadrilineatus* (stippled) and in those of the agamous generation of *Cynips longiventris* (stippled, second line).

seminationis ♂ and June 7th to July 15th for the summer-generation from galls of *A. quadrilineatus* ♂. In the instance of *A. seminationis* ♂ the *nervosus*-wasps emerge in the second year of the gall, while in that of *A. quadrilineatus* they emerge in the first year of the gall.

The flight period for *S. nervosus* in England was recorded by Askew (1961, fig. 6) to last from the beginning of May to the end of October.

Tables with host species and phenological data for various species of *Synergus*, concluded.

		England	Germany	The Netherlands	
				summer-gen. I (s)	spring-gen. II (p)
TABLE XIX. <i>Synergus thaumacerus</i> .					
<i>Neuroterus tricolor</i>	♂♀	+	-		-
<i>Neuroterus quercusbaccarum</i>	♂♀	+	-		-
<i>Trigonaspis megaptera</i> f. <i>renum</i>	♂	+	-		(26-IV) V (29-V)
<i>Trigonaspis megaptera</i>	♂♀	+	+	(15-VI) VI-VII	(20-VII)
TABLE XX. <i>Synergus nervosus</i> .					
<i>Cynips quercusfolii</i>	♂	+	<i>tacheiki</i>	-	6-VI, 17-VI
<i>Cynips longiventris</i>	♂	-	-	-	(10-V) V (4-VI)
<i>Cynips divisa</i>	♂	+	-	-	(24-IV) V (12-VI)
<i>Andricus ostreus</i>	♂	+	<i>radiatus</i> (9-IX)	IX (18-IX)	13-V
<i>Andricus curvator</i>	♂♀	+	-	12-VI, 23-VI	-
<i>Andricus curvator</i> f. <i>collaris</i>	♂	+	-	-	20-IV
<i>Andricus solitarius</i>	♂	+	-	(23-VII) VIII (15-VIII)	-
<i>Andricus quercusramuli</i>	♂♀	-	-	27-VI	-
<i>Andricus albopunctatus</i>	♂	+	-	11-VI	-
<i>Andricus callidoma</i>	♂	+	-	9-IX	-
<i>Andricus nudus</i>	♂♀	-	-	30-IX	-
<i>Andricus nudus</i> f. <i>malphigii</i>	♂	-	-	-	7-IV
<i>Andricus seminationis</i>	♂	+	-	-	21-VI
<i>Andricus quadrilineatus</i>	♂	+	-	(7-VI) VI (15-VII)	-
<i>Andricus kollari</i>	♂	-	-	-	6-VI
<i>Andricus corruptrix</i>	♂	-	-	-	30-IV
<i>Neuroterus tricolor</i>	♂♀	+	-	10-VII	-
<i>Neuroterus quercusbaccarum</i> f. <i>lenticularis</i>	♂	-	<i>tacheiki</i>	-	-
<i>Neuroterus quercusbaccarum</i>	♂♀	-	<i>radiatus</i>	-	-
<i>Neuroterus albipes</i> f. <i>laeviusculus</i> var. <i>reflexus</i>	♂	-	<i>radiatus</i>	-	-

Synergus albipes Hartig (table 21, fig. 82)

Larvae of *S. albipes* live with a number together in one gall of *Neuroterus quercusbaccarum* ♂♀. The young larvae lie scattered throughout the gall-tissue, as in most other species of *Synergus* here treated (*rotundiventris* and *apicalis* excepted). The full-grown larvae make subsidiary cells. The date of emergence is about one month later than that of the host. In the beginning of July the first galls of *Andricus ostreus* ♂ are available for the spring-generation of *albipes*; here again, the host wasps emerge much earlier than the inquilines.

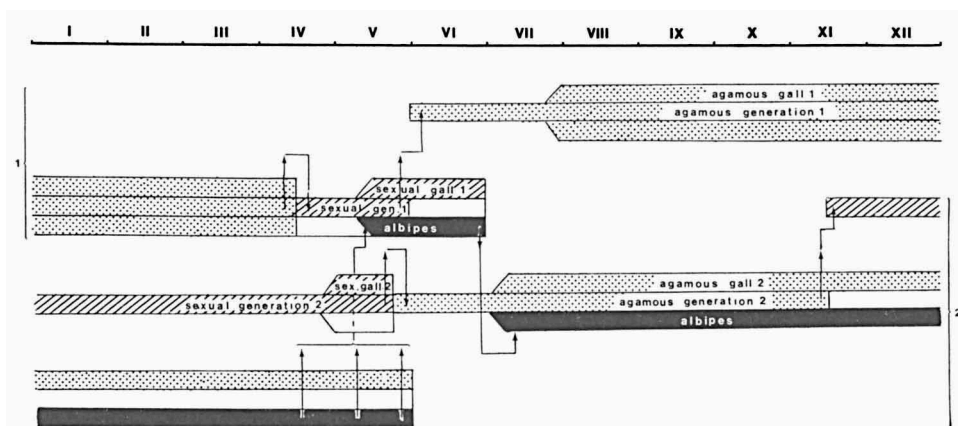


Fig. 82. Life-cycle for *Synergus albipes* (black) in the galls of the sexual generation of *Neuroterus quercusbaccarum* (shaded) and in those of the agamous generation of *Andricus ostreus* (stippled).

Synergus mutabilis Dettmer (1924: 147), described from galls of *Cynips divisa* ♂ collected at Slagharen (The Netherlands, province of Overijssel), proves to be the same as *Synergus albipes*. The type-series, consisting of three males and one female, is being preserved in the collections of the Natuurhistorisch Museum, Maastricht.

Synergus sp. B (table 22, fig. 83)

Here, as in the instance of sp. A (p. 313), the status of the form indicated by "B" is not yet established. It was reared from the agamous galls of *Cynips quercusfolii*, together with *Synergus pallicornis*, *gallae-pomiformis*, *nervosus* and *albipes*.

The wasps are robust, 3-3.5 mm in length; the shape of the head is trapezoid as in *pallicornis*, with which it also has in common the presence of distinct carinae on the vertex. The antennae however, are quite different, as

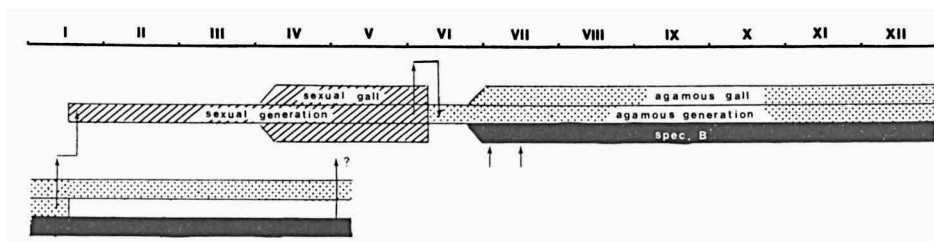


Fig. 83. Life-cycle for *Synergus* sp. B (black) in the galls of the agamous generation of *Cynips quercusfolii* (stippled).

the length-width ratio of the second segment is distinctly smaller in both sexes, and the male third segment is thickened and expanded from the middle of its length (fig. 45). These characters of the antennae give sp. B some resemblance to *S. albipes*, from which it differs in several characters, viz., the carinae on the frons and vertex (figs. 5, 6, 17), the filiform shape of the whole antennae (not more or less clavate), the dark colour of the antennae (often with light apices) and the legs, the length of the median scutal line, the male ventral plate and the genitalia, and the total size.

The extremely wide base of the median scutal line in some instances reminds one of *gallaepomiformis* (p) and the same applies to the total size and the dark colour of antennae and legs. Species B, however, has no punctures on frons and vertex, and the shape of the antennae is quite different (figs. 28, 29, 45); the carinae on the mesoscutum are irregular in sp. B, weak in *gallaepomiformis*. Differences with *nervosus* are found in the antennae, in which the second segment is rather short and the third male segment distinctly expanded, in the shape of the head (trapezoid), and in the expansion of the median scutal line, which is triangulate at its base. Askew (1961) mentioned *nervosus* as an inhabitant of galls of *Cynips quercusfolii* ♂, although less common than in *divisa* ♂ and *longiventris* ♂. In Holland it is decidedly rare in *quercusfolii*, as I have only two samples, as against about half a hundred of sp. B.

In its larval biology, sp. B is even more distinct than in its adult morphology. It is the only species ¹⁾ of which one does not find the eggs or young larvae dispersed in the gall tissue, but around or in the central cavity of the host instead. Eggs can be found in July up to the 15th, the first stage larvae till August, 20th. One of these larvae is growing faster than the others, some of which may even seem not to grow at all: there may be a difference in size

¹⁾ *S. apicalis* and *rotundiventris*, of which I did not find young stages, possibly excluded.

Tables with host species and phenological data for various species of
Synergus, concluded.

		England	Germany	The Netherlands	
TABLE XXI. <i>Synergus albipes</i> .					
				summer-gen. I (s)	spring-gen. II (p)
<i>Cynips quercusfolii</i>	♂	-	-	-	(24-IV) V (22-V)
<i>Cynips longiventris</i>	♂	-	-	5-VIII	(16-V) VI (22-VI)
<i>Cynips divisa</i>	♂	+	<i>mutabilis</i>	19-VII, 25-VIII	(8-V) V (22-VI)
<i>Cynips disticha</i>	♂	+	+	1-VIII, 8-VIII	15-VIII
<i>Andricus ostreus</i>	♂	+	<i>tristis</i>	21-IX, 23-IX	(11-IV) IV, V (29-V)
<i>Andricus curvator</i>	♂♀	+	-	(12-VI) VI (2-VII)	-
<i>Andricus solitarius</i>	♂	-	-	-	1-VI
<i>Andricus quercusramuli</i> f. <i>autumnalis</i>	♂	-	-	-	11-IV, 27-IV
<i>Andricus callidoma</i>	♂	-	-	9-IX	-
<i>Andricus nudus</i> f. <i>malphigii</i>	♂	-	-	-	(7-IV) IV (8-V)
<i>Andricus quadrilineatus</i>	♂	+	-	27-VI	-
<i>Andricus kollari</i>	♂	-	-	-	(4-VI) VI (15-VII)
<i>Andricus lignicola</i>	♂	-	-	-	31-V
<i>Andricus corruptrix</i>	♂	-	-	-	19-VI
<i>Neuroterus tricolor</i> f. <i>fumipennis</i>	♂	-	+	-	-
<i>Neuroterus quercusbaccarum</i> f. <i>lenticularis</i>	♂	+	-	-	14-V, 15-VII
<i>Neuroterus quercusbaccarum</i>	♂♀	+	+	(15-VI) VI (23-VI)	-
<i>Neuroterus numismalis</i>	♂	-	+	-	-
<i>Neuroterus numismalis</i> f. <i>vesicator</i>	♂♀	+	-	-	-
<i>Neuroterus albipes</i> f. <i>laeviusculus</i>	♂	-	+	-	-
<i>Trigonaspis megaptera</i> f. <i>renum</i>	♂	+	-	-	(10-IV) IV (20-IV)

TABLE XXII. <i>Synergus</i> sp. B.					
<i>Cynips quercusfolii</i>	♂	-	-	(30-IV) V (10-V)	

of three or four times. Eventually, towards the end of August, one finds in the centre of the gall the dry skin of the *Cynips* and besides it a cavity with the larger *Synergus* and several other, smaller larvae. In September, this results in one *Synergus*-larva per gall, or incidentally two, actively moving around in the central cavity. Adults were reared in the next year, in the end of April and in May. This leaves a gap of almost two months before the young oak-apples are again available (fig. 83).

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